

Research Note

Induction of stomatal oscillations in grape leaves: Determination by gas exchange measurement

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Key words: stomatal patchiness, stomatal conductance, oscillation, hydraulic signal.

Introduction: Stomatal pore width has been shown to vary substantially in different parts of the grape leaf (DOWNTON *et al.* 1988, DÜRING 1992, reviews: TERASHIMA 1992, POSPISILOVA and SANTRUCEK 1994, DÜRING and STOLL 1996 a, b). This so-called ‘stomatal patchiness’ can be caused by water stress (DOWNTON *et al.* 1988 a), high evaporative demand (DÜRING 1992), salinity (DOWNTON *et al.* 1990), alteration of light intensity under glasshouse and field conditions (DÜRING and LOVEYS 1996) and abscisic acid application (DOWNTON *et al.* 1988 b), suggesting that stomatal patchiness is a common phenomenon. Preliminary results obtained with grapevine leaves indicated asynchronous, uncoordinated stomatal movements in neighbouring patches (DÜRING and STOLL 1996 b). They can be synchronized and coordinated by abrupt perturbances in the water status or mesophyll CO₂ concentration as indicated by stomatal oscillations over larger portions of the leaf area (COWAN 1977, CARDON *et al.* 1994, SIEBKE and WEIS 1995). While synchronization within single patches was initiated by ‘hydraulic interaction between adjacent stomata’ (HAEFNER *et al.* 1997, MOTT *et al.* 1997), the origin of communication among stomata of several patches remains obscure.

This paper describes the induction of stomatal oscillations over larger portions of the leaf area by an abrupt increase in the transpiration rate of other leaves. There is some evidence that the synchronization of stomatal movements of several patches depends on the vine water status.

Material and Methods: Three-year-old potted Phoenix vines (*Bacchus* x *Villard blanc*) grafted to Kober 5 BB were transferred from the glasshouse to the laboratory one week before the experiments were started. During this time the well-irrigated vines with an average shoot length of 1.60 m were exposed to 320 $\mu\text{mol quanta}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ provided by two Osram HQI lamps (400 W) for 14 h·d⁻¹. Room temperature ranged from 18 (night) to 24 °C (day), relative air humidity from 40 to 55 %. Gas exchange measurements were performed with a ‘Miniküvetten-System’ (Walz, Effeltrich, Germany; for details: DÜRING 1993) at 880 $\mu\text{mol quanta}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$,

400 ppm CO₂, 23 °C leaf temperature and 13 °C dew point. Gas exchange data sets were recorded automatically every 5 min (Fig. 1) or each min (Fig. 2). Wind produced by a tower ventilator had a speed of $3.0 \pm 0.5 \text{ m}\cdot\text{s}^{-1}$ at the site of leaves. All experiments were repeated three times.

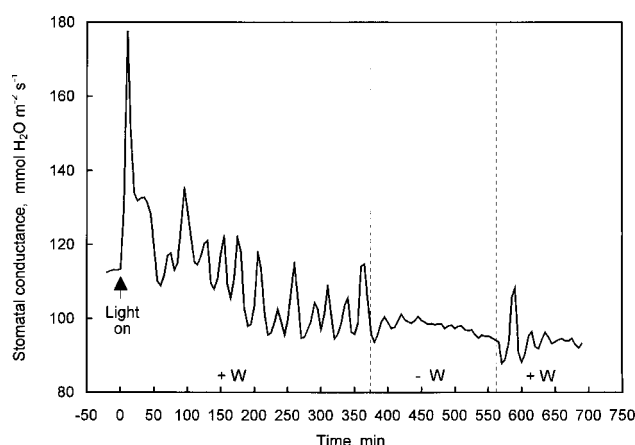


Fig. 1: Stomatal conductance of a vine leaf inserted in a cuvette and kept under constant conditions. All other leaves were permanently exposed to light and alternatively to wind (+W) or no wind (-W).

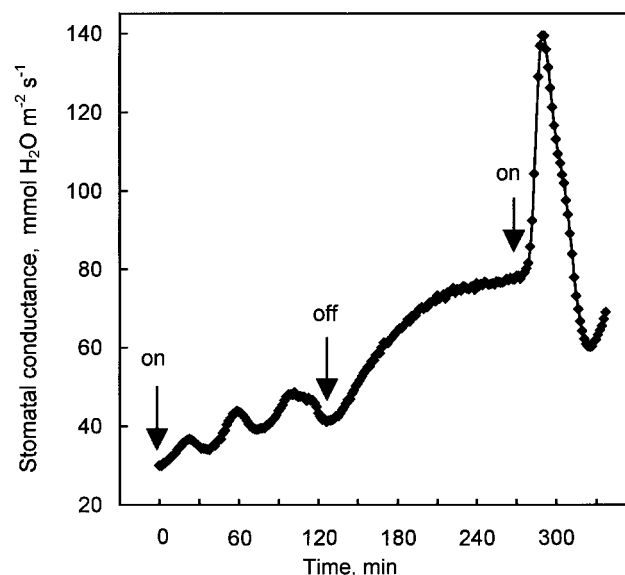


Fig. 2: Stomatal conductance of a vine leaf inserted in a cuvette and kept under constant conditions. The drought-stressed vine was irrigated and left in the dark before the onset of the experiment. At time = 0 the leaves outside the cuvette were exposed to light and wind (‘on’) or to no wind and no light (‘off’).

Results and Discussion: Previous experiments had demonstrated significant stomatal movements caused by abrupt changes of xylem pressure in detached petioles (DÜRING 1993). In intact vines xylem pressure can be altered by a sudden increase of the transpiration rate of leaves, e.g. by exposure to wind. At the onset of the present experiments one out of 12 leaves of a vine was inserted into the cuvette for gas exchange measurements and kept under constant light, temperature and air humidity conditions, while the other leaves were kept in the dark. Fig. 1 demonstrates that stomata of the experimental leaf started to oscillate when the other leaves of the vine were abruptly exposed to light and wind (+W), i.e. to conditions which

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usually cause evaporation rate to increase. In the light but without wind (-W), oscillations were dampened but recovered for a short while when the ventilator was switched on again (+W). It is assumed that an abrupt decrease in leaf turgor due to high transpiration initiated a coordination of stomatal movements, *i.e.* stomatal oscillations in the experimental leaf. Simultaneous measurements of gas exchange of a second leaf of the vine inserted just below the experimental leaf showed oscillations which were synchronous with those of the experimental leaf (data not shown). Thus, it appears that stomatal movements are coerced to coordination by 'turgor waves' running through the plant (RASCHKE 1970).

In a subsequent experiment drought-stressed vines (pre-dawn water potential -0.61 MPa) were irrigated and left in the dark for one hour to initiate stomatal closure. While the measuring leaf was enclosed in the cuvette and kept at constant light, temperature and air humidity all other leaves were abruptly exposed to light and wind ('on'). Fig. 2 demonstrates oscillating stomatal movements of the measuring leaf which started when the transpiration rate of leaves outside the cuvette was suddenly raised due to light and wind. After about 2 h when light was switched off and wind was stopped ('off') oscillations ceased while stomatal conductance values increased. This increase which was more significant compared to the first part of the experiment was probably due to stomatal closure of the leaves outside the cuvette and, hence, to a more rapid increase in the vine water status. When, after more than 4 h of recovery from drought, the leaves outside the cuvette were exposed to light and wind ('on') stomatal movements started to oscillate again, but this time the amplitude was distinctly larger.

These results corroborate earlier findings (DÜRING 1993) and indicate that turgor-dependent hydraulic signals are transmitted not only within single patches (HAEFNER *et al.* 1997) but also over larger portions of the leaf area and between various leaves. They appear to coordinate stomatal movements over larger portions of the leaf area and between different leaves. It cannot be excluded that the 'spontaneous' oscillations found under constant ambient conditions in the cuvette in earlier experiments (DÜRING and STOLL 1996) may have also been due to yet unknown ambient perturbations of the leaves outside the cuvette, *e.g.* wind produced by the automatic air condition system of the laboratory.

Conclusion: The present results demonstrate the induction of a coordinated stomatal behaviour over larger portions of the leaf area determined by gas exchange measurements. In previous results obtained with *Glechoma* oscillations over larger portions of the leaf area were assumed to be generated from already existing oscillations

in single patches by synchronization (SIEBKE and WEIS 1995). Compared to single patches, oscillations in larger portions of the leaf area can be regarded as an exception to the rule, *i.e.* they appear to be a transient phenomenon. However, since for methodical reasons oscillating movements of single stomata are difficult to analyse, a transient coordination of stomatal movements may enable studies on the physiological background of stomatal oscillations.

At the onset of gas exchange experiments, especially under conditions of changing environment, it is often difficult to achieve a steady state of gas exchange although the measuring leaf area is kept under constant conditions in the cuvette. This may be ascribed to stomatal conductance, transpiration and turgor changes in leaves other than the experimental leaf, *i.e.* to hydraulic signals.

- CARDON, Z. G.; MOTT, K. A.; BERRY, J. A.; 1994: Dynamics of patchy stomatal movements, and their contribution to steady state and oscillating stomatal conductance calculated using gas-exchange techniques. *Plant Cell Environ.* **17**, 995-1007.
- COWAN, I. R.; 1977: Stomatal behaviour and environment. *Adv. Bot. Res.* **4**, 117-228.
- DOWNTON, W. J. S.; LOVEYS, B. R.; GRANT, W. J. R.; 1988 a: Non-uniform stomatal closure induced by water stress causes putative non-stomatal inhibition of photosynthesis. *New Phytol.* **110**, 503-509.
- -; - -; - -; 1988 b: Stomatal closure fully accounts for the inhibition of photosynthesis by abscisic acid. *New Phytol.* **108**, 263-266.
- -; - -; - -; 1990: Salinity effects on the stomatal behaviour of grapevine. *New Phytol.* **116**, 499-503.
- DÜRING, H.; 1992: Low air humidity causes non-uniform stomatal closure in heterobaric leaves of *Vitis* species. *Vitis* **31**, 1-7.
- -; 1993: Rapid stomatal and photosynthetic responses of *Vitis berlandieri* leaves after petiole excision in water. *Vitis* **32**, 63-68.
- -; LOVEYS, B. R.; 1996: Stomatal patchiness of field-grown Sultana leaves: Diurnal changes and light effects. *Vitis* **35**, 7-10.
- -; STOLL, M.; 1996 a: Stomatal patchiness of grapevine leaves. I. Estimation of non-uniform stomatal apertures by a new infiltration technique. *Vitis* **35**, 65-68.
- -; STOLL, M.; 1996 b: Stomatal patchiness of grapevine leaves. II. Uncoordinated and coordinated stomatal movements. *Vitis* **35**, 69-71.
- HAEFNER, J. W.; BUCKLEY, T. N.; MOTT, K. A.; 1997: A spatially explicit model of patchy stomatal responses to humidity. *Plant Cell Environ.* **20**, 1087-1097.
- MOTT, K. A.; DENNE, F.; POWELL, J.; 1997: Interactions among stomata in response to perturbations in humidity. *Plant Cell Environ.* **20**, 1098-1107.
- POSPISILOVA, J.; SANTRUCEK, J.; 1994: Stomatal patchiness. *Biol. Plant.* **36**, 481-510.
- RASCHKE, K.; 1970: Stomatal responses to pressure changes and interruptions in the water supply of detached leaves of *Zea mays* L. *Plant Physiol.* **45**, 415-423.
- SIEBKE, K.; WEIS, E.; 1995: Assimilation images of leaves of *Glechoma hederacea*: Analysis of non-synchronous stomata related oscillations. *Planta* **196**, 155-165.
- TERASHIMA, J.; 1992: Anatomy of non-uniform leaf photosynthesis. *Photosynth. Res.* **31**, 195-212.